

The population structure of the lichen *Lobaria pulmonaria* in the middle boreal forests depends on the time-since-disturbance

Roman V. Ignatenko & Viktoria N. Tarasova

Department of Botany and Plant Physiology, Petrozavodsk State University, 33 Lenin St., 185910 Petrozavodsk, Russia.

E-mails: ocean-9@mail.ru, tarasova1873@gmail.com

Abstract: The population structure of the lichen *Lobaria pulmonaria* (L.) Hoffm. was analyzed in the Vodlozersky National Park (Karelia, Russia), for middle boreal forest stands having a time-since-disturbance spanning 80 to 450 years. To estimate the age of the last disturbance, a method of evaluation for the tree population structure was applied. The forest stand communities belonged to a successional series: middle-aged aspen – mixed aspen-spruce – pre-climax spruce – climax (old-growth) spruce forest. All thalli (1055) of *L. pulmonaria* from all substrate units (165, separately standing or lying trees and shrubs) were described within 7 sample plots of 1 ha. For each thallus, the area (cm²) and the functional-age group were determined. The number of *Lobaria* thalli per ha, number of substrate units, number of substrate types (living, standing dead and lying dead trees of different species) colonized by *L. pulmonaria*, as well as number of substrate types on which the lichen had completed its life cycle increased with time-since-disturbance.

Keywords: *Lobaria pulmonaria*; middle boreal forest; succession; population ecology

INTRODUCTION

Lobaria pulmonaria (L.) Hoffm is a large epiphytic cyanolichen that is widely distributed within and beyond the Holarctic region (Yoshimura, 1971), and which inhabits old-growth forests in the boreal region. The species is considered extremely sensitive to anthropogenic impact and is used as an indicator of ecological continuity of habitats (Rose, 1992). Over the past 60 years, the world population of *L. pulmonaria* has declined considerably and at present time it is endangered in many countries of Western Europe (Gauslaa, 1995; Zoller et al., 1999; Gu et al., 2001; Jüriado & Liira, 2009; Mikryukov et al., 2010; Scheidegger et al., 2012). In Russia this lichen is listed in the Red Data Book of the Russian Federation (2008) as well as in many regional Red Data Books, including the Republic of Karelia (2007).

However, it has been suggested that in the forests of the north European Russia there is no threat to *Lobaria pulmonaria* now or in the immediate future, even at the current rate of forest management activity (Kravchenko & Fadeeva, 2008; Pystina & Semenova, 2009). This assumption is significant when considering the catastrophic reduction of *L. pulmonaria* populations in the other countries of northern Europe (Walser et al., 2001; Jüriado, Liira, 2010), as well as to the southern portion of north European Russia, for example, in the Leningrad

region (Istomina, 1996) and the Novgorod region (Katenina, 1999). Such favorable conclusions are often based on the analysis of the species occurrence (“presence-absence”) or the number and size of thalli in different forest types, without evaluating the population structure and the potential capacity for recovery of the species in successional forest communities.

There is still insufficient data on change in the quantitative and qualitative condition of *Lobaria pulmonaria* in forest communities at different successional stages. Previous studies examining the effect of time since last disturbance on *L. pulmonaria*, often reported the species status within two categories—disturbed (managed) forests and old-growth forests, without a clear continuum applicable to forest loss and the initial conditions of forest regeneration (Gu et al., 2001; Scheidegger et al., 2012). However, some researchers have dealt with the longer-term dynamics of *L. pulmonaria* populations at the level of large spatial units (landscapes) (Snäll et al., 2005). This approach is based on meta-population theory, which is represented as a network of interrelated local populations within a landscape or region (Hanski, 1999). According to this theory, the population persistence for certain species of epiphytic lichens depends on three important factors: the conditions of the region or landscape (natural conditions, the

history of economic development, the level of anthropogenic impact), characteristics of forest communities (the structure of the tree stand, the proportion of phorophytes in the tree stand, the time since last disturbance) and features of dispersal ability (predominant mode of reproduction and distance of diaspores dispersal) (Johansson, 2006). In the boreal forest, it has been emphasized that the frequency of catastrophic disturbances has great importance for the conservation of populations: high frequency disturbance reduces the number of individuals because of decreasing time necessary for growth and dispersal, while the frequency leads to a decreasing number in the new generation of deciduous trees and therefore suitable substrate for lichens (Snäll et al., 2005).

Lobaria pulmonaria in European Russia occurs in different types of forests, but the prevailing number of locations is reported in coniferous forest communities (Potasheva & Kravchenko, 1995; Istomina, 1996; Kravchenko & Fadeeva, 2008; Fadeeva & Kravchenko, 2008; Pystina & Semenova, 2009; Ignatenko & Tarasova, 2015; Ivanova, 2015, and others). Within this context, *L. pulmonaria* colonizes the bark of different trees and moss-covered rocks. In the forest communities of European Russia the main host tree for *L. pulmonaria* is aspen (Istomina, 1996; Kravchenko & Fadeeva, 2008; Ivanova, 2015, etc.).

It is known that aspen forms secondary forests after the destruction of spruce communities, and is also included in old-growth spruce forests (Volkov, 2008). Epiphytic species colonize tree trunks, which are ephemeral habitat patches, and these species must track the dynamic patch network for their long term survival at the landscape level (Snäll et al., 2005). Population dynamics of epiphytic species is thus closely related to the dynamics of phorophytes in tree stands, and therefore to the forest dynamic in general. It is known that at least 400–450 years are required for total recovery of the climax spruce forest after disturbance in the middle boreal subzone in Northwest Russia (Gromtsev, 2008).

The aim of this study was to explore the quantitative parameters of the *Lobaria pulmonaria* thalli (occurrence, abundance, size), as well as the functional-age condition and substrate preferences of the species, in forest communities at different succession stages in the territory of the Vodlozersky National Park.

MATERIALS AND METHODS

Study area

The research was carried out in forest communities of the Karelian part of the Vodlozersky National Park located in Northwest Russia, during 2014–2015 (Fig. 1). Vodlozersky National Park is the largest (468,300 ha) protected area in the territory of Northwest Russia, as well as in Europe as a whole (Fig. 1). The park is located in two regions: Arkhangelsk region (337,600 ha) and in the Republic of Karelia (130,600 ha). The Park area includes Lake Vodlozero and an extensive basin of the Ilekka River, which is the lake's main tributary (mainly in Arkhangelsk region).

The Park territory is located in the middle boreal subzone and characterized by variation of forests, swamps and aquatic ecosystems that reflect the natural boreal zone of north European Russia. The climate is temperate, transitioning from maritime to continental, with short, cool summers and prolonged winters. The annual average air temperature is + 3 °C and the annual average precipitation ranges from 450 to 750 mm (Romanov, 1961). The relief is low and flat, heavily waterlogged and only in the northern portion of the Park rises to the low-mountain ridge of Vetreny Poyas (up to 350 m).

The Vodlozersky National Park includes one of the largest areas in Europe of middle taiga covered with old-growth forests (Chervjakov, 2001). In the Karelian part of the Vodlozersky National Park there is predominant spruce (*Picea abies*, *P. obovata*, *Picea x fennica*) occupying 58% of the territory, while pine forests account for approximately 36%. Birch (*Betula pendula*, *B. pubescens*) and aspen (*Populus tremula*) forest communities, which mostly regenerate following clear cuttings, fires and windfall of forests, as well as on abandoned cultivated fields, do not exceed 5% (Ananjev & Raevsky, 2010).

Lichenological studies in the Park area have been carried out since 1992 and a first preliminary checklist of lichens from the Karelian portion included 152 species (Tarasova & Stepanova, 2001). Recently 188 species were also reported from the Muroigora, which is located in the Arkhangelsk portion of the Park (Tarasova et al., 2016).

Study sites and data collection

The study was performed for 7 permanent sample plots each with an area 1 ha (100×100m) (Fig.

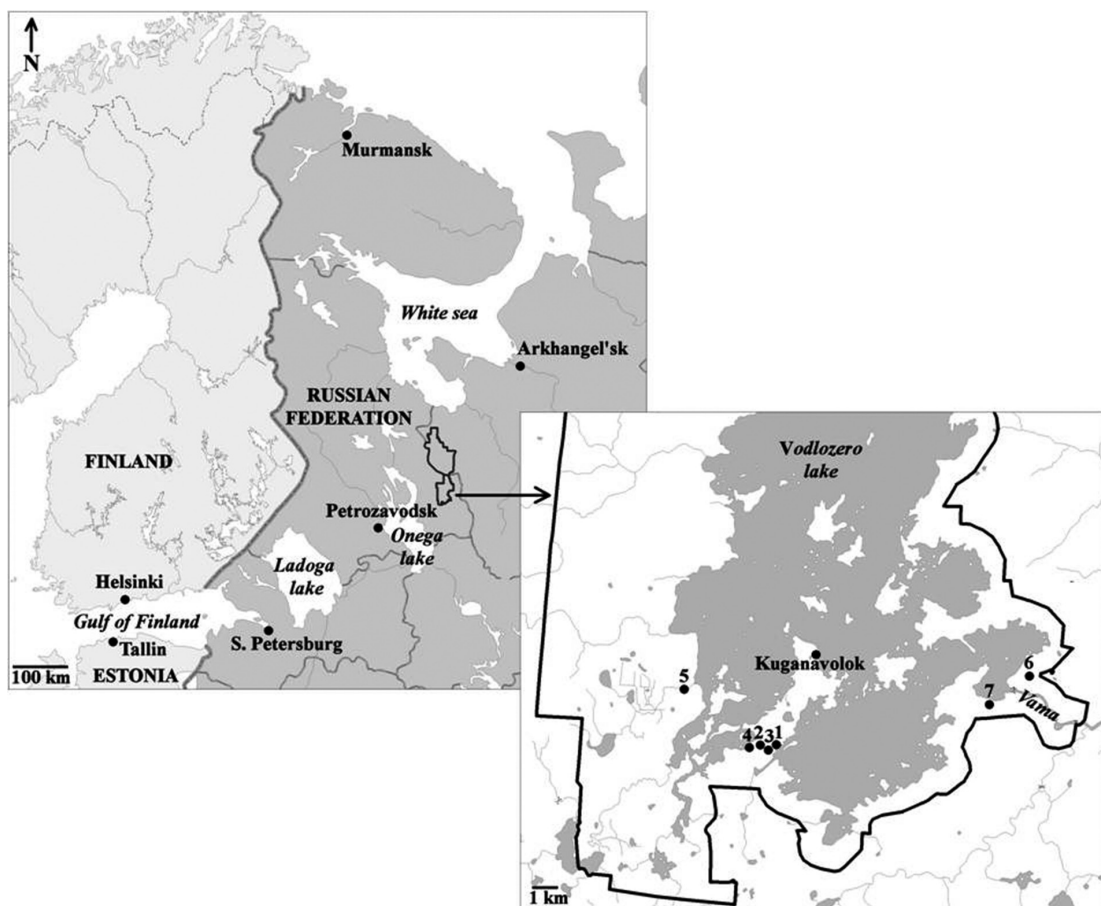


Fig. 1. The location of the study area (Republic of Karelia, NW Russia): thick line – border of Vodlozersky National Park, black circles – sample plots (additional data about sample plots see in Table 1).

1). All studied forest communities belonged to a series representing the successional pathway of recovery to climax spruce forest of the *Vaccinium myrtillus* – green mosses sub-type. The plots occurred on plains with a loamy moraine and without stagnant moistening. The spruce forests after fire or clear cutting mostly recover by means of a gradual change in tree species, usually transitioning through birch or aspen stands (Kazimirov, 1971; Dyrenkov, 1984). On richer soils the successional pathway includes aspen, and on poorer soils birch (Ipatov, 1960; Degteva et al., 2001).

In the current investigation, we consider the pathway of recovery for spruce forests through the aspen stage. The time-since-disturbance of

the studied forest communities was established as stages of succession ranging from 80 to 450 years, with composition, structure and values for their main characteristics significantly different (Table 1). Based on established data for succession of middle boreal spruce forests (Kazimirov, 1971, Dyrenkov, 1984), the forest communities were categorized into four groups corresponding to different successional stages: 1) middle-aged aspen forest *Vaccinium myrtillus* – *Calamagrostis arundinacea* type; 2) mixed aspen-spruce forest *Calamagrostis arundinacea* – *Vaccinium myrtillus* type; 3) preclimax spruce forest *Vaccinium myrtillus* – green mosses type; 4) climax (old-growth) spruce forest *Vaccinium myrtillus* – green mosses type (Table 1).

Table 1. The main characteristics of studied forests in Vodlozersky National Park

Type of forest	No of sample plot	GPS coordinate	Age of the last disturbance, years	Basal area, m ² ha ⁻¹	Basal area, m ² ha ⁻¹ standing dead trees	Basal area, m ² ha ⁻¹ fallen dead trees	Proportion in the tree stand, %		Age of trees, years	
							Spruce	Aspen	Spruce	Aspen
Middle-aged aspen forest <i>Vaccinium myrtillus</i> – <i>Calamagrostis arundinacea</i> type	1	62°12.001'N 36°51.114'E	80	29.0	1.0	2.0	8	47	28–48	26–73
	2	62°11.976'N 36°49.659'E	100	30.3	0.6	0.5	27	45	25–95	56–103
Mixed aspen-spruce forest <i>Calamagrostis arundinacea</i> – <i>Vaccinium myrtillus</i> type	3	62°11.972'N 36°51.009'E	160	26.5	3.6	1.5	53	22	28–84	83–151
	4	62°12.076'N 36°50.249'E	180	31.0	3.9	3.9	65	14	48–143	67–151
Preclimax spruce forest <i>Vaccinium myrtillus</i> – green mosses type	5	62°13.448'N 36°45.222'E	260	19.3	2.4	5.8	64	2	46–229	128–152
Climax (old-growth) spruce forest <i>Vaccinium myrtillus</i> – green mosses type	6	62°13.545'N 37°05.081'E	410	22.8	1.0	3.1	81	12	24–263	164–198
	7	62°13.026'N 37°03.456'E	450	29.3	0.8	4.8	89	9	31–180	109–203

To estimate time-since-disturbance in the studied communities, we evaluated the population structure of each tree stand (mainly spruce trees) following N. I. Stavrova et al. (2016). Thus, in the corners of sample plots we established a circular area with a radius of 2–10 m, and measurements for all trees and seedlings (species, height, diameter of the trunk, age) were recorded. The age of 20–25 trees with different trunk diameters and heights was determined using an increment borer, and for the remaining trees using calibration curves. Based on this data, the distribution patterns for the amount and the supply of wood for spruce (*Picea abies*, *P. obovata*, *Picea x fennica*) and aspen (*Populus tremula*) were plotted.

The age of the last disturbance for aspen and mixed spruce-aspen communities with a threshold less than 120 years was determined as the maximum age of the oldest trees. In fact, in these communities, aspen and spruce stands are formed in one generation by trees of the same age (Kazimirov, 1971).

Considering the fact that in preclimax and old-growth spruce forests these trees of the first generation are often lost to mortality, the age of the last disturbance was estimated based on the population structure of the tree stand. For

example, old-growth spruce forests with the age of the last disturbance older than 400 years are characterized by differently-aged trees (stands with a continuum of tree ages, up to a maximum age for spruce > 270 years), with a predominance of young spruce trees (up to 90–95%) and an equal wood supply over each age class in the stand (no more than 15% in each class) (Kazimirov, 1971; Stavrova et al., 2016). These tree age profiles were compared to data from the literature, for which time-since-disturbance had been determined for studied communities.

All *Lobaria pulmonaria* thalli occurring on all types of substrates, at heights of 0–2 m from the ground were recorded, in 7 sample plots of 1 ha. For each thallus of *L. pulmonaria* the total area (cm²) was estimated using a frame (25×25 cm), as well as determining the functional-age group according to Mikhailova (2005): sterile (*st*) – without reproductive structures; hyposorediate (*s1*) – with marginal soralia; mesosorediate (*s2*) – with abundance of marginal and single laminar soralia; hypersorediate (*s3*) – with marginal soralia; fertile (*fert*) – with apothecia; subsenile (*s/sen*) – with partly destroyed thallus in centre and with regenerative structures; senile (*sen*) – with dying lobes on which regenerative struc-

tures arise as a result of the destruction of larger thallus. The following data for sample plots were evaluated: the total number of substrate units, the total number of standing or fallen trees and shrubs colonized by *L. pulmonaria*, the number of substrate types, the number of colonized tree species and their condition (living, dead standing, dead fallen). We thus defined trees of the same species in one of three possible states: living, dead or fallen tree.

The statistical processing of the results was based on a single-factor regression analysis using the linear model $y = ax + b$ (Ivanter & Korosov, 2011) in the program package of Microsoft Office Excel (2007).

RESULTS

In the spruce forests of Vodlozersky National Park, with a successional series running through the stage of an aspen tree stand, *Lobaria pulmonaria* occurred after 80 years from the last disturbance. In younger aspen forests (< 80 years) *L. pulmonaria* was not found. The earliest occurrence is for middle-aged aspen forest *Vaccinium myrtillus* – *Calamagrostis arundinacea* type with spruce seedlings. For the total area of the studied forest communities (7 ha), 1055 thalli of *L. pulmonaria* were recorded on 165 substrate units. The number of thalli in the different forest communities varied greatly: from 33 to 309 samples per ha. The thallus area of *L. pulmonaria* also varied significantly, from 1 cm² to 1200 cm².

Total and average numbers of thalli

The average number of thalli per unit of substrate and the abundance of thalli in communities (thalli/ha) was related to the time since the last forest disturbance (Fig. 2.1). With the increasing time, in the communities aged from 80 to 450 years, the number of *Lobaria pulmonaria* thalli increased six-fold – from 50 to 300 (Fig. 2.1). The minimum abundance of thalli per hectare (33, 87) was recorded in the middle-aged aspen communities. In mixed spruce-aspen forests, the abundance of thalli increased to 107, 118 thalli/ha. In preclimax and climax spruce forests the maximal abundance of thalli was recorded, and reached 139 and 262, 309 thalli per 1 ha, respectively (Table 2). Moreover, in these communities an average of 10 and 7 thalli occurred on each unique substrate unit, respectively (Table 2).

Numbers of substrate units and substrate types

The number of substrate units increased with increasing time since the last disturbance from 9 pcs/ha in middle-aged aspen forests to 44 pcs/ha in the climax spruce forests. The average number of substrate units was 24 pcs/ha (Fig. 2.2).

In the studied forest communities *Lobaria pulmonaria* occurred on a wide range of substrates (Table 2). According to our results, 76% of the substrate units (living, dead, fallen trees) colonized by this lichen were represented by a deciduous tree species: *Populus tremula* L. (59%), *Sorbus aucuparia* L. (32%), *Betula* sp. (8%), *Alnus incana* (L.) Moench (1%). A proportion of coniferous trees, such as *Picea* sp., and of *Juniperus communis* L., accounted for 24% of the total number of substrate units.

With the increasing time-since-disturbance, from 80 to 450 years, the number of substrates colonized by *Lobaria pulmonaria* increased from 5 to 8 ($R^2 = 0.67^*$). Moreover, the substrate preferences of *L. pulmonaria* changed with the increasing time-since-disturbance. In the middle-aged aspen forests thalli usually colonized the trunks of living aspen trees with an age of 56–143 years (22%), as well as rowan trunks with an age of 23–92 years (36%) (Tab. 2). In mixed aspen-spruce forests *L. pulmonaria* was often found on large aspen trees aged 67–181 years (56%) and on standing dead aspen trees (16%) and rowan (24%). In preclimax spruce forest, 63% of thalli were recorded on standing dead of aspen, and 22% on old aspen trees aged 128–152 years. In the climax (old-growth) spruce forests thalli of *L. pulmonaria* had begun to actively colonize the branches of young spruce trees aged 13–67 years (Fig. 3).

The number of thalli on spruce trees increased during forest succession, and maximum values were observed in old-growth spruce forests with an age of 410–450 since their last disturbance, in which case the proportion of lichen thalli found on spruce was 45–51% of the total thalli number (Fig. 2.3, Table 2).

Area of thalli

The average area of the thalli of *Lobaria pulmonaria* decreased with increasing age since the last disturbance. The average area of the thalli during the period 80–450 years since distur-

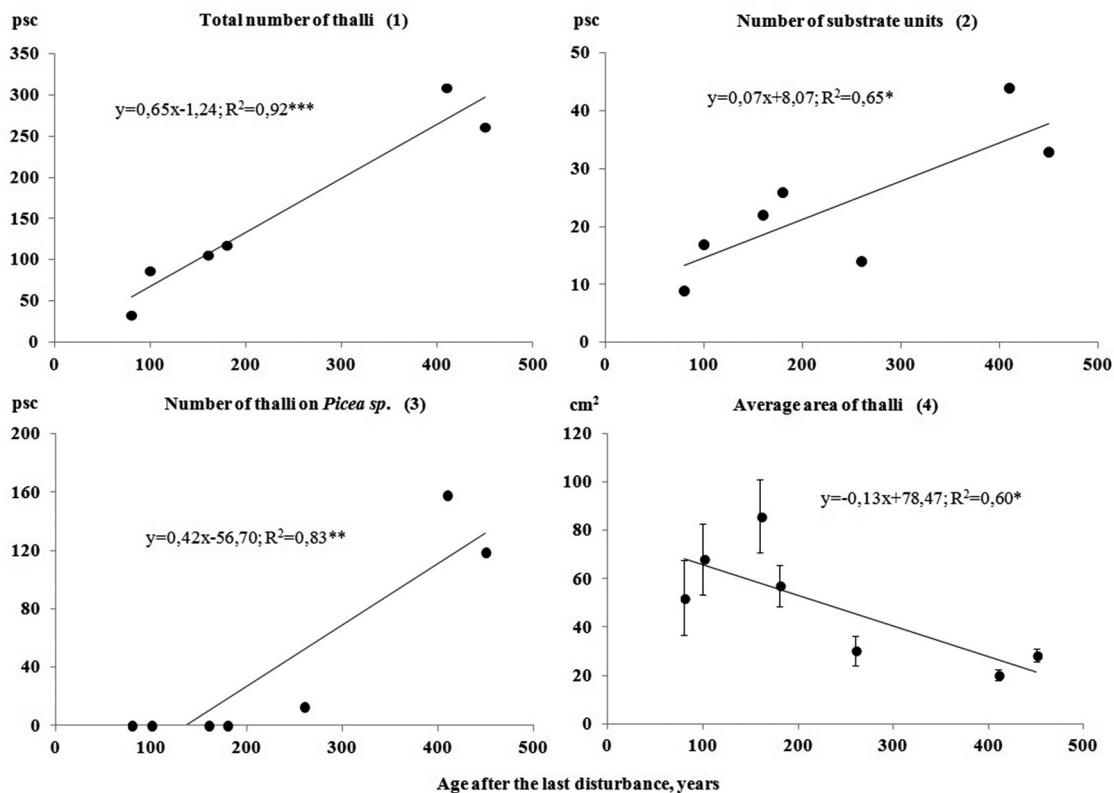


Fig. 2. Quantitative parameters for *Lobaria pulmonaria* in forest communities with different time periods since the last disturbance. P-value of regression coefficient (R^2) is less than the significance level, such as 0.001 (***) or 0.01 (**) or 0.05 (*).

bance decreased by a factor of 2.5, from $60.1 \pm 15.1 \text{ cm}^2$ to $24.3 \pm 2.5 \text{ cm}^2$ (Fig. 2.4). This is related to a change in the proportion of young, medium-sized individuals of *L. pulmonaria* contributing to the total number of thalli. Thus, in middle-aged aspen communities, the proportion of thalli with area less than 51 cm^2 was 78% of the total number of thalli, while in old growth spruce forests it was 90%. In middle-aged aspen forest communities the proportion of *L. pulmonaria* thalli with an area more than 358 cm^2 was 5%, and in spruce-aspen communities 9%, while in climax spruce forests 0.4% (Fig. 4).

Functional age-related groups of thalli

All functional-age groups were represented within *Lobaria pulmonaria* populations in the study area. However, in the middle-aged aspen forests, *L. pulmonaria* did not form the full functional-age spectra on its main host tree,

Populus tremula (Table 3). In these communities the thalli of *L. pulmonaria* had a complete cycle of development from sterile to senile individuals on the living trees of *Sorbus aucuparia*. In mixed aspen-spruce forests full functional-age profiles for populations of *L. pulmonaria* were found on the trunks of living *P. tremula* and on dead standing trees of *S. aucuparia* and in preclimax spruce forest on dead and living *P. tremula*. In climax spruce forests, full functional-age profiles were recorded on trunks of living and dead standing *P. tremula* and living *Picea* sp. (Table 3).

In the studied forest communities, the number of thalli with apothecia varied from 0 to 12 pcs/ha. The absence or minimal density of thalli with apothecia (0–2 pcs/ha) was observed in the middle-aged aspen forests and in preclimax spruce forest. The maximum values (9–12 pcs/ha) were recorded in forests where age since disturbance corresponded to spruce-aspen

Table 2. Substrate types, number of colonized trees and *Lobaria pulmonaria* thalli (in brackets) in studied forests in Vodlozersky National Park

Substrate types	Number of trees, number of thalli (in brackets)						
	Middle-aged aspen forest type		Mixed aspen-spruce forest type		Preclimax spruce forest type	Climax (old-growth) spruce forest type	
	1	2	3	4	5	6	7
<i>Betula</i> spp. (living)	3 (12)	–	–	–	1 (2)	4 (17)	–
<i>Betula</i> spp. (standing dead)	–	–	–	–	–	2 (2)	–
<i>Picea</i> spp. (living)	–	–	–	–	3 (13)	15 (128)	11 (119)
<i>Picea</i> spp. (standing dead)	–	–	–	–	1 (5)	4 (28)	–
<i>Picea</i> spp. (fallen dead)	–	–	–	1 (3)	–	2 (15)	–
<i>J. communis</i> (living)	–	1 (5)	–	–	–	–	–
<i>J. communis</i> (standing dead)	1 (2)	–	–	–	–	–	–
<i>A. incana</i> (living)	–	–	–	–	–	–	1 (5)
<i>A. incana</i> (fallen dead)	–	–	–	–	–	–	1 (12)
<i>P. tremula</i> (living)	3 (10)	5 (16)	13 (60)	15 (65)	4 (30)	4 (34)	7 (70)
<i>P. tremula</i> (standing dead)	–	–	4 (11)	2 (7)	4 (88)	3 (34)	4 (32)
<i>P. tremula</i> (fallen dead)	–	1 (6)	2 (15)	1 (4)	–	2 (3)	–
<i>S. aucuparia</i> (living)	1 (8)	4 (35)	1 (5)	–	1 (1)	4 (9)	5 (12)
<i>S. aucuparia</i> (standing dead)	–	2 (9)	1 (11)	6 (33)	–	2 (5)	3 (11)
<i>S. aucuparia</i> (fallen dead)	1 (1)	4 (16)	1 (5)	1 (6)	–	2 (4)	1 (1)
Total (per 1 ha)	9 (33)	17 (87)	22 (107)	26 (118)	14 (139)	44 (309)	33 (262)
Number of substrate types	5	6	6	6	6	11	8

**Fig. 3.** Thalli of *Lobaria pulmonaria* on branches of young *Picea* spp. in the climax spruce forest *Vaccinium myrtillus* – green mosses type.

communities and old growth forests. However, in forest communities with time-since-disturbance of 160–180 years the proportion of fertile thalli reached 9%, while in old-growth spruce forests its was only 4%.

DISCUSSION

The results of the present study show that time since the last forest disturbance affects significantly the quantitative and qualitative parameters of *Lobaria pulmonaria* populations. During the succession of forest communities, the structure of the tree stand and microclimatic conditions change (Snäll et al., 2005).

It is known that the life-cycle of *Lobaria pulmonaria* takes on average 35 years (Scheidegger et al., 1998; Scheidegger & Goward, 2002). This species reproduces mainly by means of vegetative diaspores (soredia, isidioid soredia) leading to a high density of thalli within habitat of suitable conditions without disturbances (Öckinger

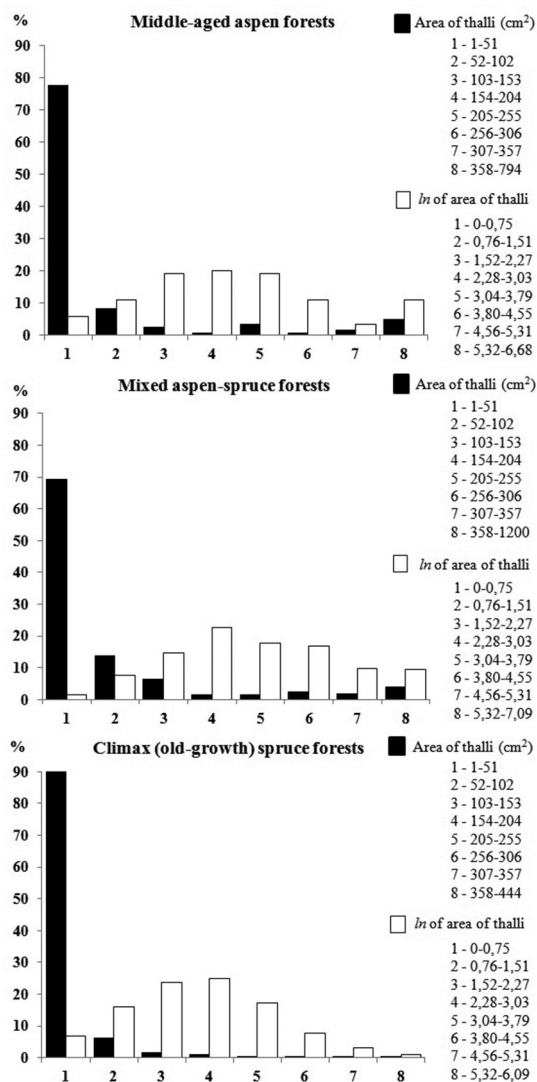


Fig. 4. Distribution of *Lobaria pulmonaria* thalli (%) by area (dark shading) and by the natural logarithm of the area (no shading) in communities with different time since the last disturbance.

et al., 2005). The vegetative dispersal distance of *L. pulmonaria* is only 15–30 m (Jüriado et al., 2011). According to numerous reports, *L. pulmonaria* most often colonizes the trunks of large deciduous trees with a rough bark (Gu et al., 2001; Jüriado et al., 2011, 2012; Brunialti et al., 2015), which might be considered as a limiting factor in the distribution of this species.

In the conditions of Vodlozersky National Park, *Lobaria pulmonaria* occurs only in forest communities with an age of more than 80 years after the most recent disturbance. These communities are characterized by dense stands in which deciduous tree species predominate (72–93%). Moreover, middle aged and mature aspen trees contribute up to 46% of these tree stands. In these communities, with an average value for basal area of 14 m²ha⁻¹ and a density of crowns at 87–90%, large aspens of 90–100 years can be colonized by *L. pulmonaria*. It has been reported from studies in boreal-nemoral communities that the occurrence of *L. pulmonaria* is recorded in forests aged 40–60 years (Jüriado & Liira, 2009). These authors concluded that, in addition to old-growth forests, the potential habitat of *L. pulmonaria* could be eutrophic boreo-nemoral medium-aged forest communities, with large deciduous trees. The age of these reported trees are less than is typical for phorophytes colonized by the species in less productive forests. However their size and the structure of bark surface is suitable for colonization by *L. pulmonaria*. In such forest communities the tree stands have high a density and their structure resembles the structure otherwise observed in old-growth forests (Jüriado & Liira, 2009). Thus, such relatively younger forest communities might serve as corridors that connect areas of old-growth forests in a spatial network. Moreover they could play a significant role in maintaining the population of *L. pulmonaria* at a landscape level.

With the increasing time-since-disturbance, changes in the structure of the tree stand occur: the proportion of aspen in the stand decreases, and the proportion of spruce and its density increase. This leads to the transformation of habitat conditions, mainly through changes in the level and quality of light intensity and humidity (Protopopov, 1975; Gauslaa et al., 2007). In aspen forests, the light intensity and the level of insolation throughout the year vary greatly due to leaf fall in autumn. Experiments carried out in southern Norway demonstrated that the growth of *Lobaria pulmonaria* occurred throughout the year, but the maximum increase in biomass and area was observed from July to September (Larsen et al., 2012). It is known that intense direct sunlight can cause chlorophyll degradation in the *L. pulmonaria* thalli, and the consequences affect the growth of the species (Gauslaa et al., 2007). In the old-growth spruce forests, due to

Table 3. The profile of functional-age groups for *L. pulmonaria* populations on its main host trees *Picea* spp. (*Pic. spp.*), *Populus tremula* (*Pop. trem.*) and *Sorbus aucuparia* (*Sor. auc.*) in the forests of Vodlozersky National Park

Type of forest	No s. p.	Substrate types	Number of thalli in different age groups ¹							Proportion of thalli (%)
			st	s1	s2	s3	fert	s/sen	sen	
Middle-aged aspen forest type	1	<i>Pop. trem.</i> (living)	9	0	0	0	0	1	0	30
		<i>Sor. auc.</i> (living)	8	0	6	0	0	0	2	48
	2	<i>Pop. trem.</i> (living)	10	3	0	0	0	3	0	18
		<i>Sor. auc.</i> (living)	15	6	1	2	2	3	6	40
Mixed aspen-spruce forest type	3	<i>P. tremula</i> (living)	16	19	1	1	4	8	11	56
		<i>Sor. auc.</i> (standing dead)	1	6	0	0	2	1	1	10
	4	<i>Pop. trem.</i> (living)	9	27	5	2	3	7	12	55
		<i>Sor. auc.</i> (standing dead)	12	4	5	2	5	3	2	28
Preclimax spruce forest type	5	<i>Pop. trem.</i> (living)	13	6	5	1	0	2	4	22
		<i>Pop. trem.</i> (standing dead)	39	25	7	8	1	3	4	63
Climax (old-growth) spruce forest type	6	<i>Pic. spp.</i> (living)	103	47	3	0	5	0	0	51
		<i>Pop. trem.</i> (living)	7	5	0	0	4	0	18	11
		<i>Pop. trem.</i> (standing dead)	3	12	3	1	2	2	11	11
	7	<i>Pic. spp.</i> (living)	68	45	2	2	2	0	0	45
		<i>Pop. trem.</i> (living)	3	24	2	7	3	4	27	27
		<i>Pop. trem.</i> (standing dead)	2	9	1	5	3	0	11	12

¹full names of functional age-related groups see in Material and methods

the edificatory role of spruce and the occurrence of several levels of tree canopy, a relatively stable microclimate occurs throughout the year. As a result of gap-dynamics, sunlight is diffuse, and the air is more often and more continuously saturated with water vapor, which contributes to a longer period of hydration for *L. pulmonaria* thalli (Merinero et al., 2014).

Meanwhile, in middle-aged aspen forests, with less stable microclimatic conditions during the year, populations of *Lobaria* are smaller and substrates types are less favorable. In these communities, the *L. pulmonaria* thalli mainly colonize the living trunks of aspen and rowan. In mixed spruce-aspen communities with an age of 160–180 years since the last disturbance, numerous large aspens (the main phorophyte of *Lobaria*) with roughened bark exist, which contribute to an increase in the number of thalli and their area. After the decay of a single-aged aspen tree stand (as a result of the successional change from aspen to spruce forests), in forest communities of 260–450 years, *L. pulmonaria* loses a significant portion of its

favourable substrates. In fact, in old-growth forests aspen occurs only in the gaps of the wind-thrown complexes and its proportion in the overall tree stand decreases. In the spruce forest communities with an age of 260 years since the last disturbance the majority of thalli (63%) were recorded on standing deadwood of aspen. Due to the favorable microclimatic conditions in these undisturbed communities *L. pulmonaria* begins to colonize a larger range of trees of different species and condition, including the lower branches of young spruce trees, which, even as a temporary substrate, can significantly increase the potential of the lichen for further dispersal in the forest community.

It was found during studies in the boreal forests of Canada, that young coniferous trees with the lower branches inhabited by *Lobaria pulmonaria* are located in the so-called “drip-zone” of large old aspen (Goward & Arsenault, 2000). The authors suggested that leaching of various compounds with precipitation from the upper part of the tree crowns of nutrient-rich aspen affected the coniferous trees with their

crowns located below. As a result of this process the total mineral composition and pH of bark for coniferous trees increased. Thus, these species of tree, which are characterized by poor mineral composition and acidic bark normally, become a potential substrate for colonization by epiphytic cyanolichens, which have requirements for high pH values and suitable humidity conditions (Goward & Arsenault, 2000). The researchers suggested that the “drip zone effect” is a widespread phenomenon, but it is observed only in humid communities. As a result of our studies, it was found that in spruce forests with an age of 410–450 years, the proportion of *L. pulmonaria* thalli on spruce was 45–51% of the total. All the coniferous trees on which the lichen was recorded were situated within a radius 1–6 m of a large aspen, and as consequence confirming the above hypothesis.

It has been established that with an increase of age since last disturbance from 80 to 450 years in spruce communities recovering through the aspen forest stage, the substrate preferences of *Lobaria pulmonaria* change. The lichen species shifts the substrate in which it completes a life cycle. In the aspen forest, full functional-age profiles might be observed only on the trunks of living *Sorbus aucuparia*, in mixed spruce-aspen communities on *Populus tremula* and standing deadwood of *S. aucuparia*, and in subclimax spruce forest on living and standing deadwood of *P. tremula*, while in climax communities on living and standing deadwood of *P. tremula* as well as on branches of *Picea* sp.

According to the results of our studies, the maximum proportion of fertile thalli was recorded for the spruce-aspen communities, representing 9% of the total number of thalli. In these communities there was higher number of large aspens with rough bark, which contributed positively to the increasing the number of thalli and their area. We assumed that the high density of old-growth aspen raises the probability of developing genetically diverse individuals.

In fact, there is an assumption that the formation of apothecia becomes possible only in genetically heterogeneous populations (Zoller et al., 1999). Studies of *Lobaria pulmonaria* in the hemiboreal forests of Estonia revealed that in managed forests the proportion of generative individuals in the population was significantly higher in comparison with old-growth communities (the age of the dominant trees was 120–190

years) and wooded meadows (Jüriado et al., 2011). However, based on molecular genetic analysis, it has been established that the high levels of genetic diversity of *L. pulmonaria* are within undisturbed forest communities (Jüriado et al., 2011; Scheidegger et al., 2012).

In conclusion, the Vodlozersky National Park is an important reserve for the preservation of the epiphytic cyanolichen *Lobaria pulmonaria*. Within its territory there are large areas of old-growth communities, and as a result of local fires, windfalls as well as overgrowing of abandoned fields, middle-aged aspen and spruce-aspen forest communities have been formed in which suitable conditions and potential substrates for colonization are created. Due to the large area of old-growth forest communities and low forest fragmentation, the *L. pulmonaria* population at a landscape (regional) level is maintained and distributed successfully through dispersal. Results of our study show that despite the long time-since-disturbance and the reduced proportion of aspen in the tree stand, there are still enough substrates for colonization of *L. pulmonaria* in old-growth forests.

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